THE
JOURNAL
OF
RAPTOR RESEARCH

CONTENTS

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ALTITUDINAL DISTRIBUTION AND CONSERVATION OF RAPTORS IN SOUTHWESTERN COLOMBIA

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ABSTRACT.—Diurnal raptors were surveyed during four weeks along a gradient from sea level to 4000 m on the Pacific slopes of the Andes in southwestern Colombia. However, most of the work on habitat selection, density estimates and conservation problems was done within the subtropical level (1200–2400 m) in the 3200-ha forest reserve of La Planada and its surrounding mosaic of pastures, cultivated fields and disturbed forest. Twenty-two raptor species were recorded. Forest species richness does not change noticeably at successive levels between 0 and 1000 m, but this richness decreases rapidly above 1500 m. The number of open grassland species tends to increase with elevation. Extensive deforestation is a major threat to the survival of several forest raptors, including endemics from the humid western slope of the Andes. Some sufficiently large areas of relatively undisturbed forest, suitable for raptor conservation, still remain between 500 and 2000 m but very few can be found above or below this level.

Distribución y conservación de aves de rapiña en diversos niveles de altitud en el sudoeste de Colombia

EXTRACTO.—Raptoras diurnas fueron inspeccionadas durante 4 semanas a lo largo de una gradiente comprendida entre el nivel del mar y los 4000 metros, en las pendientes andinas del Pacífico en el sudoeste de Colombia. Sin embargo, la mayor parte del trabajo de selección de habitat, estimaciones de densidad y problemas de conservación, ha sido hecho dentro del nivel subtropical (1200–2400 m) en las 3200-ha. de la reserva forestal La Planada, y el mosaico de sus alrededores con pastos, campos cultivados y alterada floresta. 22 especies de aves de rapiña han sido registradas. La riqueza de las especies raptoras de floresta no cambia notablemente en los sucesivos niveles entre 0 y 1000 m, pero sí decrece rapidamente a partir de los 1500 m. El número de las especies de las áreas de pastos tiende a crecer con la elevación. La extensiva deforestación constituye el mayor peligro para la supervivencia de las aves raptoras de floresta; esto es cierto también para las especies de las húmedas pendientes occidentales de los Andes. Areas suficientemente grandes de floresta relativamente inalterada, apropiadas para la conservación de aves raptoras, aún se encuentran entre los 500 y los 2000 m, pero muy pocas pueden encontrarse por encima o por debajo de este nivel.

[Traducción de Eudoxio Paredes-Ruiz]

Colombia is ornithologically one of the richest countries in the world with at least 1695 species of birds reliably recorded, including 75 Falconiformes, as summarized by Hilty and Brown (1986). The extreme southwestern part of the country is among the least studied areas. Yet this Pacific slope of the Andes, called southern Choco, which extends into northwestern Ecuador, is both rich in endemic taxa and threatened throughout by rapid deforestation, especially in the lowlands. Moreover, diurnal raptors are usually poorly surveyed because specific sur-

vey methods are required to establish the presence, or to assess the relative abundance, of many species. These methods are time consuming and are often appropriate for only a particular subset of the raptor assemblage (Thiollay 1989a). The birds in this study area proved to be no exception.

The present study of the distribution of raptors along a gradient from sea level to 4000 m was of interest for several reasons. Little was known about the area and its endemic species; the gradient had a wide altitudinal range but within a relatively narrow
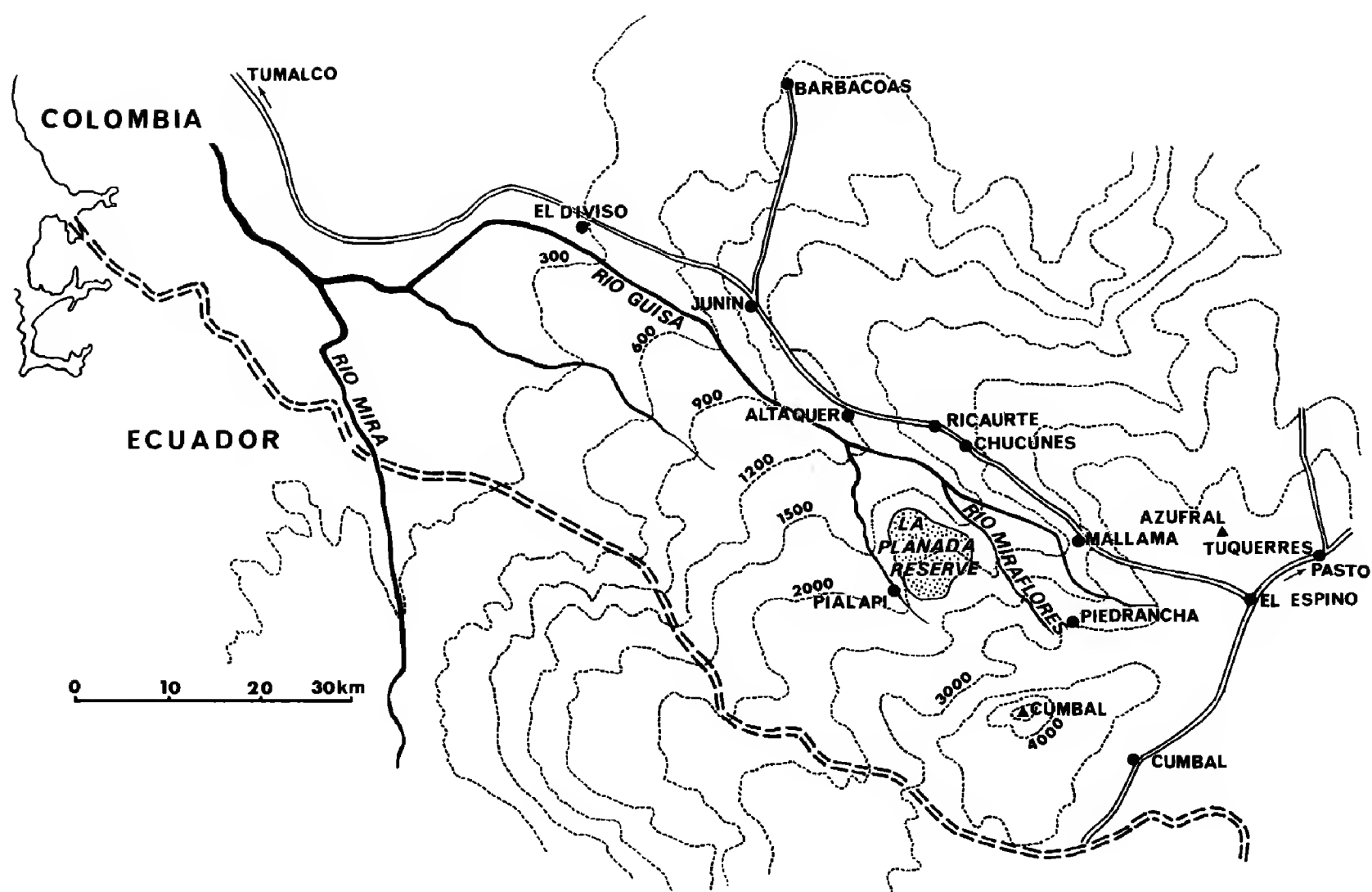
Figure 1.   Map of the study area in southwestern Narino, Colombia. Dots represent villages or small towns and triangles the highest peaks (volcanoes).

strip; comparative data were drawn in 1987 from a personal survey of raptors in nearby northwestern Ecuador; this was among the first uses of raptors as sensitive indicators for the management of a Biosphere Reserve (UNESCO-MAB) proposed in the area; several species may soon become extinct because of the current high rate of deforestation.

STUDY AREA AND METHODS

The southwestern corner of Colombia (Narino), along the Ecuadorian border, provides a 115-km-wide gradient from the upper ridge of the western Andes, dominated by the Cumbal Volcano (4764 m), down to the Pacific coast. It is crossed by the Pasto-Tumaco road of which the El Espino-Altaquer section has been the most intensively surveyed during this study (Fig. 1).

This Pacific slope of the northern Andes (Choco) has the heaviest rainfall in the Americas (Hilty and Brown 1986), ranging from over 3000 mm on the coast to an average of 10 000 mm in the foothills (500–1000 m) and decreasing to about 4–5000 mm at the subtropical and montane levels. The heavy cloud cover tends to increase with altitude. The mean temperature drops by about 6°C with each 1000-meter increase in elevation.

The altitudinal gradient was divided into five main zones

(Holdridge 1967). 1) The Paramo extends from the tree line (3200–3400 m) to the upper limit of vegetation (around 4500 m). The Rosette Shrub (*Espeletia* sp.) was characteristic of the lower part of this wet alpine grassland where some patches of low, dense *Polylepis* woodland still remained in the ravines. The upper part of the Paramo was dominated by grasslands. Strong winds, cool temperatures, moderate rains and extensive cloud cover occurred almost daily. 2) The temperate or montane forest was found mainly from 2500–3500 m between El Espino, Miraflores and Piedrancha. Trees were usually under 20 m tall and covered with epiphytes. Stunted trees and shrubs dominated a so-called elfin forest near the tree line. 3) From 2400 m down to 1200 m, a subtropical, humid or premontane forest was found. Many trees reached 25–30 m in height and were heavily covered by epiphytes (e.g., ferns, mosses, bromeliads). Trees were dominated by the genera *Cassia, Clusia, Ficus, Miconia,* as well as palms. The dense and wet undergrowth had many tree ferns. 4) From 1200 m to 500 m, in the Altaquer-Junin-Barbacoas-El Diviso area, the foothills bore a tropical wet forest (rain forest of Holdridge 1967). It was the elevation with the heaviest rainfall, covered by a dense, evergreen forest, with trees reaching 30–35 m. The highest tree species diversity may be found at this level (C. Samper, pers. comm.). 5) Below 500 m, the lowland wet forest was the tallest (35–45 m) with comparatively less undergrowth and still high tree species

richness. A wide belt of mangroves fringed the coast. All along the gradient, much of the original forest cover has been converted to cattle pastures and cultivated fields; shrubs predominated on lightly grazed or abandoned areas.

Most of my observations were made in and around La Planada Natural Reserve, within the subtropical zone. This 3200-ha reserve was at an altitude of 1500 to 2200 m and covered with primary forest. Over 200 ha were regenerating, after being either converted into pasture or logged for valuable timber 10–20 years ago. The mature forest was on average 20–30 m high with a dense, very wet undergrowth and a discontinuous canopy. Palms and tree ferns were numerous and epiphytes were omnipresent. Two hundred resident bird species have been identified (unpubl. list from numerous observers), including 25 Choco endemics. Mammals (squirrels, monkeys, carnivores) usually existed at low densities. The largest mammals were the Spectacled Bear, *Tremarctos ornatus* and the Brocket Deer, *Mazama americana*.

On the eastern border of the reserve, the deep valley of Pialapi was partly cleared for shifting cultivation and the remaining forest patches were often disturbed. Along the northeastern side, the slopes of the Rio Miraflores valley were used for cattle ranching, but substantial areas of forest still covered the upper slopes. The large valley of the Rio Guiza was densely populated and cultivated, with pastures on the upper slopes. Some patches of forest remained only on the steepest slopes, ridges and ravines. The lower and upper parts of the valley are here defined from the position of La Planada (at the level of Chucunes-Ricaurte) 25–30 km downstream to Altaquer and upstream to Mallama. The upper valley was more deforested but less cultivated than the lower section.

The entire area of La Planada-Pialapi and the valley from Altaquer to Mallama were surveyed on foot between 24 June and 26 July 1988. Three additional days were spent in the montane zone (around Cumbal and Azufral Volcanoes) and two days in the lowlands. Rain and fog were of almost daily occurrence and lowered the detectability of raptors. Using all available trails and roads, I searched the area for raptors from dawn to dusk, making intensive use of clear late morning hours. I spent more time in openings (treefall gaps, landslides, clearings, ridges) from where most raptors could be seen in flight. The secretive forest falcons (*Micrastur* sp.) were mostly located by their calls in early and late hours.

The data were expressed as the mean number of individuals recorded per hour spent under three different conditions affecting raptor detectability and defined as optimal, suboptimal and unsuitable. Based on prior experience (Thiollay 1989a), and according to the behavior of each species, these conditions included: habitat (i.e., inside or outside the forest), time of day and weather. A mean frequency of occurrence per hour was then calculated, using only optimal conditions. This index of abundance was comparable within a given species between different localities but not between species, which usually vary widely in their behavior and conspicuousness.

Most of La Planada Reserve was covered in this survey and all resident species are thought to have been recorded or confirmed by previous records. Conservative density estimates are presented based on the mapping of all observations and the behavior of adult birds monitored. This minimum number of pairs of each species is probably too low for the secretive small forest species but much more accurate for the conspicuous large soaring species. Pairs of displaying *Leucopternis* or *Leptodon* and even calling *Micrastur* were widely separated and thus easy to distinguish from each other without a complete mapping of their territory.

Around the 3000-ha forest of La Planada, an additional area of about 7000 ha of mixed pastures, cultivated fields, old clearings and disturbed forests was surveyed mainly for easily detectable (soaring) species. A minimum number of pairs was estimated for this total area of approximately 10 000 ha (see species status). The aim of the census was to provide some basic data about the ecological requirements of such species if their survival is to be considered in a future management plan for this part of the western Andes. More details about census are given elsewhere (Thiollay 1989a).

RESULTS

Altitudinal Distribution. The distribution of raptors along the altitudinal gradient is presented in Figure 2. It was not possible to give a more quantitative picture of the species' distribution because of the brevity of the survey in the foothills and lowlands. Table 1 emphasizes the relative abundance of species in the subtropical-temperate zone where most of the work was carried out. Below I describe the raptor assemblage in each successive altitudinal zone but species will be cited only in the upper level of their range and not repeated in each of the following ones (see Fig. 1). Especially in the least surveyed areas, some species may have been overlooked. This is why I mention the species that I have not seen but that have been recorded by J. Orejuela (pers. comm.) or that were known formerly and are still likely to exist at similar level in western Narino (Hilty and Brown 1986).

In the Paramo zone, the Carunculated Caracara (*Phalcoboenus carunculatus*) was still common and widespread in the highest grasslands and often came down to 3000 m or lower into ploughed fields. The Red-backed Hawk (*Buteo polyosoma*) was even more common, but was mostly associated with the lower paramo (up to 3800 m) and the montane grasslands down to 1800 m and even 1600 m in the La Planada area. Although considered merely a non-breeding migrant in Colombia by Hilty and Brown (1986), I found this species breeding on the slopes of the Azufral Volcano, above El Espino. An adult brought prey to a nest near the tree line at 3400 m on 7 July and another adult was followed by a calling, newly fledged young. Two Cinereous Harriers (*Circus ci-*

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                        TROPICAL                              MONTANE

                Lowland   Foothill   Subtropical   Temperate   Paramo
Altitude (meters)  0       1000        2000          3000       4000
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Cathartes aura
Coragyps atratus
Leptodon cayanensis
Chondrohierax uncinatus
Elanoides forficatus
Elanus leucurus
Circus cinereus
Accipiter striatus
Accipiter collaris
Accipiter superciliosus
Accipiter bicolor
Leucopternis princeps
Leucopternis semiplumbea
Geranoaetus melanoleucus
Buteo magnirostris
Buteo brachyurus
Buteo polyosoma
Oroaetus isidori
Phalcoboenus carunculatus
Herpetotheres cachinnans
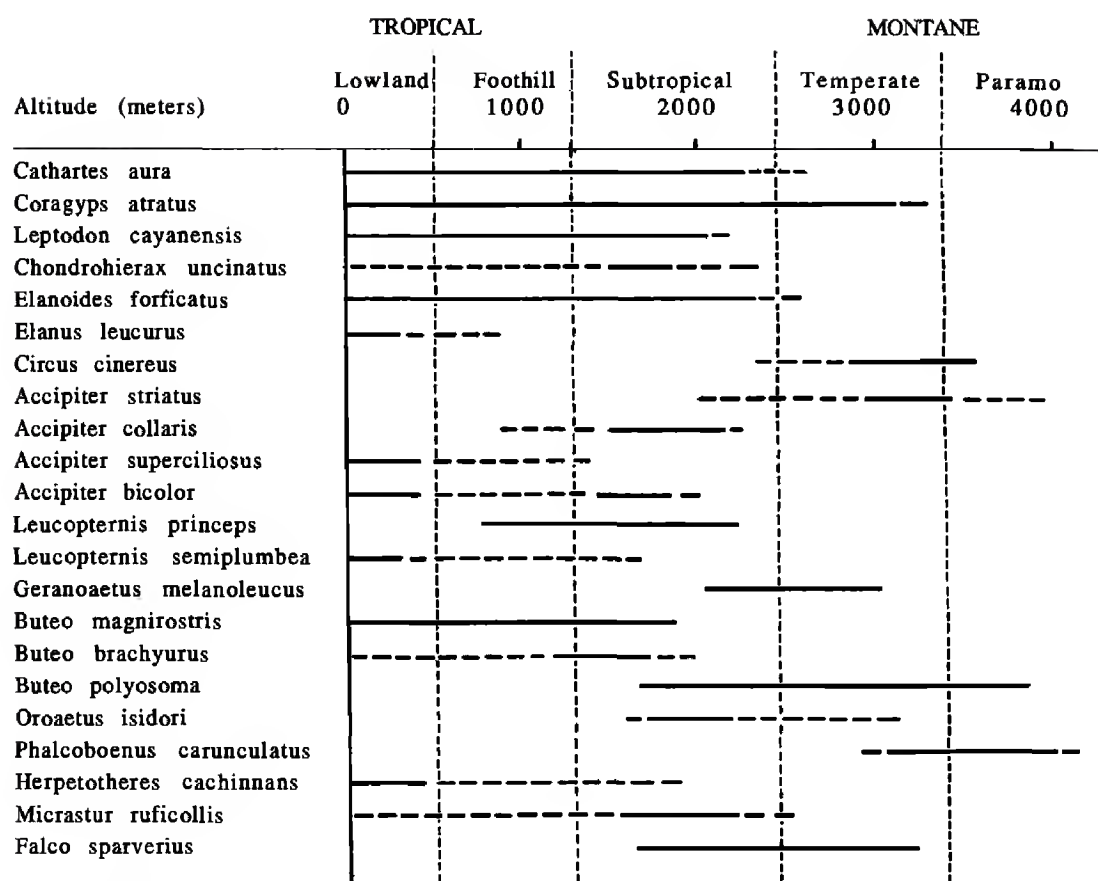Micrastur ruficollis
Falco sparverius

Figure 2. Altitudinal distribution of Falconiformes recorded in July 1988 along the Pacific slope of the Andes in southern Colombia. Solid lines represent regular observations. Dashed lines are ranges cited by Hilty and Brown (1986) but not confirmed during this study, or personal observations that are out of the known breeding level given by these authors. Fifteen additional species were formerly reported and are still likely to occur in the area, mainly in lowland forest.

Table 1. Raptor population of the subtropical zone in southwestern Narino, Colombia. Numbers represent the percentage of optimal detectability hours in which the species were recorded. Mean number of individuals seen per hr are in parentheses. The five habitats are arranged in increasing order of visually estimated deforestation. The total number of suitable census hrs ranged from 11–101.

	LA PLANADA RESERVE 1500–2200 m	PIALAPI VALLEY 1200–1900 m	RIO MIRAFLORES 1500–3300 m	LOWER RIO GUIZA 1200–1500 m	UPPER RIO GUIZA 1600–2500 m
Coragyps atratus		14 (2.0)	72 (4.2)	82 (4.1)	75 (5.3)
Cathartes aura		14 (1.0)	24 (1.0)	55 (1.8)	12 (4.0)
Leptodon cayanensis	28 (1.0)	20 (1.0)			
Chondrohierax uncinatus	20 (2.0)				
Elanoides forficatus	30 (1.0)	43 (6.7)	24 (5.6)	37 (18.3)	
Accipiter collaris	6 (1.0)	3 (1.0)			
Accipiter bicolor	4 (1.0)				
Leucopternis princeps	30 (1.5)	72 (1.8)	73 (2.2)		
Leucopternis semiplumbea	1 (1.0)				
Geranoaetus melanoleucus					25 (2.0)
Buteo magnirostris	14 (1.0)	57 (2.2)	79 (2.2)	45 (1.8)	12 (2.0)
Buteo brachyurus			9 (1.0)	12 (2.0)	
Buteo polyosoma			27 (1.3)		14 (1.0)
Oroaetus isidori	14 (1.0)				
Micrastur ruficollis	17 (1.1)				
Falco sparverius					38 (1.3)
Species richness	10	7	7	5	6
Diversity index (H')	2.150	1.376	1.582	1.143	1.106

nereus) were seen in the lower paramo and meadows of the same area. The Andean Condor (*Vultur gryphus*) formerly widespread (Goodfellow 1902), is now very rare in Narino (Orejuela, pers. comm.) and was not seen. It is still present in northern Ecuador (pers. obs.).

In the temperate montane zone, numerous Black Vultures (*Coragyps atratus*) were foraging in the cattle pastures and cultivated fields. They occurred up to 3300 m in the Cumbal-Espino-Tuquerres valley and were common in densely populated areas all along the gradient down to the coast. The American Kestrel (*Falco sparverius*) was locally common from 3200 m down to 1600 m. Two pairs of Black-chested Buzzard-Eagles (*Geranoaetus melanoleucus*) were located in the upper Rio Guiza valley around 2500 m and 2900 m. The nest of one of them, on a cliff ledge, contained a fully feathered fledgling on 17 July. I saw other pairs in similar grassy and rocky slopes near cliffs above El Pedregal and in the Rio Pasto Canyon near Chachagui. The only temperate forest raptor recorded was the Sharp-shinned Hawk (*Accipiter striatus*) between 3000 m and 3500 m. Three individuals, including one in dark phase, were hunting around a 200-ha forest remnant, along edges, shrubby areas, pastures and lower paramo at the foot of the Azufral Volcano. A feather was even found by C. Samper (pers. comm.) at 4000 m. The White-throated Hawk (*Buteo albigula*) which is a typical species of similar temperate forests in northern Ecuador, has not been observed here and is not cited from Narino (Hilty and Brown 1986).

In the subtropical zone, the Turkey Vulture (*Cathartes aura*), which was more common in the lowlands, extended here up to 2200 m and occasionally 2600 m but it was less numerous at this elevation than the Black Vulture. The Gray-headed Kite (*Leptodon cayanensis*) reached its upper limit at this level (2100-2200 m). It may breed up to 1900 m where a display flight was recorded, but it was more common in the coastal plain. The Hook-billed Kite (*Chondrohierax uncinatus*) which was seen at 1800-2000 m, may not be breeding at this upper limit of its range. The Swallow-tailed Kite (*Elanoides forficatus*) was seen commonly between 1200 and 2400 m, sometimes in flocks of 11 to 32 individuals. It was less abundant in the deforested lowlands. The little-known Semicollared Hawk (*Accipiter collaris*) and the much more conspicuous Barred Hawk (*Leucopternis princeps*) were the two most characteristic species of this altitudinal level and among the most

frequent. I saw a pair of Barred Hawks down to 800 m below Junin. The Semi-collared Hawk is also known to extend down to the foothills (Hilty and Brown 1986). I observed both species up to 2200 m. The Bicolored Hawk (*Accipiter bicolor*) probably reaches its upper limit at La Planada Reserve where I recorded it several times around 1700 m. I saw it also in the lowlands and thus its range overlaps completely with that of *Accipiter superciliosus* and with most of that of *A. collaris*. The Roadside Hawk (*Buteo magnirostris*) was the most common hawk in the cleared semi-wooded areas, from sea level to 1900 m. It overlapped with the American Kestrel in the upper 200-300 m of its range. Individuals of the Short-tailed Hawk (*Buteo brachyurus*) were occasionally seen hunting up to 1900 m, but the highest established pair was recorded at 1300-1400 m. The White-rumped Hawk (*Buteo leucorrhous*) has been recorded in the La Planada area, but was not seen during this study. The Black-and-chestnut Eagle (*Oroaetus isidori*) is a rare, spottily distributed and threatened species, typically associated with the undisturbed, wet, subtropical forest of this level. I identified it six times, only in the La Planada area. The Barred-forest Falcon (*Micrastur ruficollis*) was the only common and widespread forest falcon, seen between 1500-2200 m, and may be the most abundant raptor in the natural forest undergrowth.

In the tropical foothills, no new species were recorded. However, two presumably rare Choco forest endemics, the Plumbeous Hawk (*Leucopternis plumbea*) and the Plumbeous Forest-falcon (*Micrastur plumbeus*) are known from this area, which several lowland species also may reach (Hilty and Brown 1986).

The lowlands were visited only briefly. This area was almost entirely deforested and devoted to cattle raising and cultivation. The only remaining forest patch was too small to include a representative sample of the natural raptor community. The species not previously recorded on the gradient were the Black-shouldered Kite (*Elanus leucurus*) and the Laughing Falcon (*Herpetotheres cachinnans*) in open pastures and secondary woodlands. Both may extend to 1000 m and more. The semiplumbeous Hawk (*Leucopternis semiplumbea*) and the Tiny Hawk (*Accipiter superciliosus*) were seen in and around forest fragments. I also recorded the former once at 1600 m in La Planada Reserve but it may not be resident at that altitude. Up to 10 additional forest species were known (Hilty and Brown 1986), and are still
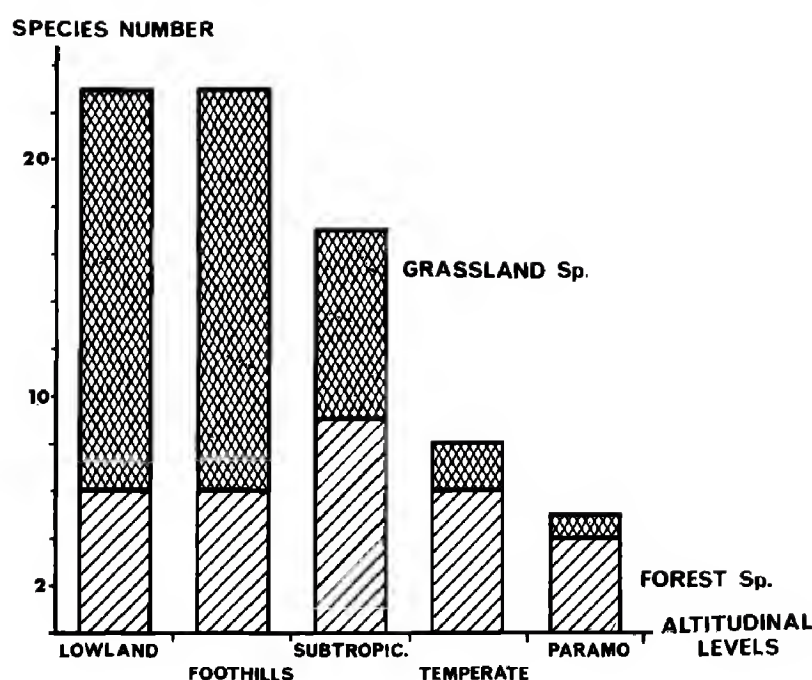
SPECIES NUMBER

Figure 3.   Highest number of primarily forest (hatched) and grassland or open-woodland species (cross-hatched) recorded in this study, or likely to occur (Hilty and Brown 1986), along the altitudinal gradient in SW Nariño. All regular species are included, regardless of their abundance or breeding status. Occasional vagrants are excluded.

likely to occur in the coastal plain. These include the Double-toothed Kite (*Harpagus bidentatus*), Plumbeous Kite (*Ictinia plumbea*), Common Black Hawk (*Buteogallus anthracinus*), Crested Eagle (*Morphnus guianensis*), Black-and-white Hawk-eagle (*Spizastur melanoleucus*), Ornate Hawk-eagle (*Spizaetus ornatus*), Red-throated Caracara (*Daptrius americanus*), Slaty-backed Forest-falcon (*Micrastur mirandollei*), Collared Forest-falcon (*Micrastur semitorquatus*) and Bat Falcon (*Falco rufigularis*). Some of them may survive in the area but at least the eagles require large areas of relatively undisturbed forest (Thiollay 1989b) that may no longer exist at low elevation.

Habitat Selection in the La Planada Area. The raptors studied may be divided into several categories according to their natural habitat and their observed susceptibility to deforestation. Obligate forest species occur only in sufficiently large areas of primary or old secondary forest. *Micrastur ruficollis* has never been seen outside dense forest undergrowth. *Oroaetus isidori* was apparently hunting only over large tracts of forest, flying directly and high above clearings and second growth. Both species are likely to be the most sensitive to forest degradation or fragmentation.

Some primary forest species may hunt regularly along edges, in some openings, second growth and disturbed forest. *Leptodon cayanensis*, *Accipiter col-

laris, *A. bicolor* and probably *Chondrohierax uncinatus* are representatives of this category. They may survive forest disturbance and fragmentation better than obligate forest species, but they do not take advantage of it and cannot persist in heavily deforested areas. Other forest species, such as *Leucopternis princeps*, are readily using, or even consistently associated with, natural or man-made openings inside the forest, including large wooded pastures along edges. *Elanoides forficatus* hunts for insects over the canopy of both unbroken and fragmented forest, as well as over open woodlands. They appear to benefit from a moderate amount of deforestation (at least *L. princeps* is rarer or absent in large unbroken tracts of forest) but they still avoid areas that are extensively cleared.

Originally nonforest species are still associated with partly wooded areas, forest edges and clearings (e.g., *Cathartes aura*, *Buteo magnirostris*, *B. brachyurus*). They increase their hunting and/or breeding range at least in the early stages of deforestation, since they readily colonize newly deforested areas. Most open grassland species invade formerly wooded areas in advanced stages of deforestation (Fig. 3). *Geranoaetus melanoleucus*, *Buteo polyosoma* and *Falco sparverius* were here typical representatives of the fauna replacing that of the former temperate forest.

The number of pairs of each species recorded during this one-month survey is probably too conservative. Some pairs may have been overlooked. However, the difference between the actual and observed densities cannot be great and is likely to provide a reasonable estimate of the current carrying capacity of the area. Two different pairs of *Leptodon cayanensis* were located on opposite sides of the 3000-ha La Planada Reserve. Their home ranges extended beyond the reserve's limits. An additional record may have represented a third pair within the 10 000-ha area. Only one pair of *Chondrohierax uncinatus* was seen flying over the reserve. One flock including 2 to 13 *Elanoides forficatus*, and sometimes additional isolated birds, were seen every day moving all over the area. The resident population within the 10 000 ha may not have exceeded 15 birds.

I made several observations within the reserve of *Accipiter collaris*, including individuals carrying prey. The existence of a minimum of two pairs can be assumed. This species was not seen outside the reserve. Similarly the presence of one pair of *Accipiter bicolor* was inferred from the spatial grouping of the six different records within the 3000-ha protected forest. However, these two secretive little hawks are

easily overlooked and their actual population may have been higher.

Leucopternis princeps was the only common large hawk. Six pairs were located on the 10 000-ha area. Three of the home ranges overlapped the limits of the 3000-ha reserve but probably none of them was completely included in it. At least seven pairs of *Buteo magnirostris* were identified, always associated with clearings. Only one pair was on the reserve. One pair of *Buteo polyosoma* with a fledged young was hunting regularly in the northern part of the study area, outside the reserve. One adult *Oroaetus isidori* was seen several times over the western and southwestern parts of the reserve, often ranging well outside the boundary of the protected area. It is unlikely that more than one pair of this rare eagle occurred within the 10 000-ha study area and the protected forest zone was apparently not large or suitable enough to meet all of its requirements.

At least, three well separated pairs of *Micrastur ruficollis* were located (direct observations and dawn or dusk calls), within the central part of the reserve. It was probably the most abundant forest raptor and the only one for which the 3000-ha reserve may be large enough to support a significant, if not self-sustainable, population.

DISCUSSION

Community Composition. Twenty-two raptor species were recorded and at least fourteen additional ones are expected. Altogether, two-thirds (24) are forest species, and only 12 are grassland or very open-woodland species. The marked succession and turnover of communities found along altitudinal gradients in the Andes (see Terborgh 1971, Terborgh and Walker 1975) were also found here, although the incomplete censuses at lower levels preclude a detailed analysis. Some species had narrow altitudinal distributions, replacing each other along the gradients while others had wider and overlapping distribution ranges (Figure 1). The genus *Accipiter* offers striking examples of three altitudinal specialists, with *A. superciliosus* under 1000 m, *A. collaris* between 1000 and 2500 m and *A. striatus* above 2500 m. The range of a larger species, *A. bicolor,* overlapped with that of *collaris* and *superciliosus.*

The total species richness, and the number of forest species, quickly decreased with altitude, but only above 1000 m (Figs. 2 and 3). At mid-level of the gradient (subtropical), the loss of forest species through deforestation was partly balanced by the

invasion of species originating from grasslands and upper levels. At this elevation, the grassland community became richer than that of the forest alone. But the overall man-induced richness of the forest-grassland mosaic was still 26% lower than that of the tropical forest alone. At higher elevation, more raptor species were favored than were lost when the forest cover was destroyed. Conversely, below about 1500 m, many more species were lost than gained through large scale deforestation. The bird assemblages of small degraded patches of woodlands among fields and pastures were probably much poorer than those of the original forest. These patterns may be explained by the former rarity of open habitats below the temperate zone and the evolution of few species adapted to open areas in the humid lowlands. Moreover, apart from paramo specialists, most of grassland species benefiting from deforestation were geographically widespread and often common species, whereas the disappearing forest birds were potentially threatened everywhere and are therefore in more urgent need of conservation.

Conservation Problems. Raptors face a major threat from the extensive and rapid deforestation at all altitudinal levels, for cattle grazing more than for cultivation. Logging is now very important everywhere (first for valuable timber, then for fuelwood and charcoal) and it often precedes and prompts forest clearing. Erosion prevents regeneration and further aggravates deforestation. Pollution and hunting pressure seemed to have only a local and minor impact.

No comparable censuses, with statistically testable results, have been made in different forest types. However, at least within the best studied area, both abundance and diversity of forest raptors decreased with the reduction and degradation of forest patches (Table 1). A higher proportion of records per unit of time or distance covered was obtained from high primary forest in the reserve, on moderate slopes with deep, well-drained soils. Unfortunately these areas are also the most accessible and are said to be the most valuable for timber production and agriculture. Therefore they are the first to be logged and cleared. The remaining forest patches tend to be of the poorest type, i.e., on steep slopes, at high elevations, in ravines, on narrow ridges or swampy flats.

The wet Pacific slope of the Andes of Colombia and western Ecuador is well known for its numerous endemic bird species. Among the Falconiformes alone, several species have restricted ranges (*Micrastur*

plumbeus, and to a lesser extent, *Leucopternis plum-bea* and *L. princeps*) or very scattered distributions (e.g., *Accipiter collaris, Oroaetus isidori*). Moreover, they are very little-known forest species whose long-term conservation may be dependent on national parks in Colombia and Ecuador which are currently in small number and understaffed.

Although the minimum size of a viable population of raptors is still debated, it can hardly be lower than several pairs. Thus the size of an isolated forest patch required for the long-term survival of a raptor population must be large. The 3200-ha reserve of La Planada harbors at best a few pairs of the most abundant species and not a single complete home range of the rarest ones. Fortunately, several species here use edges, clearings or secondary vegetation around the forest (all *Accipiter* and *Leucopternis* species) or can cross wide expanses of degraded wood-lands between primary forest patches (*Oroaetus*). The small forest falcons (*Micrastur*), although restricted to forest undergrowth, may have small territories (under 100 ha) and reach relatively high densities (this study, Klein & Bierregaard 1988, Thiollay 1989b). These behavioral traits may reduce the area of forest reserves necessary for the survival of viable populations of these species.

Within the study area, both the lowland and the temperate zones are so deforested that there is little hope of preserving a viable natural community of forest raptors or even to afford the persistence of every forest species. In the La Planada-Pialapi area, significant expanses of suitable forest still remain. If deforestation can be stopped (e.g., through a management plan of the proposed Biosphere Reserve), the original raptor community may survive. However, the best prospects for conservation lie with the large tracts of little-disturbed forest that still remain on lower slopes (500–1000 m, notably the Junin-Barbacoas area). The very heavy rainfall may prevent large scale agricultural development and most of the easily accessible timber has already been logged. It is the last opportunity to take conservation measures in an area that probably harbors most of the species of the lower and upper levels, as well as endemics of its own.

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DEVELOPMENT OF FORAGING BEHAVIOR IN THE AMERICAN KESTREL

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ABSTRACT.—We observed the development of foraging behavior after nest departure in 12 sibling groups of American Kestrels (*Falco sparverius*). Perch resting decreased whereas perch hunting, eating self-captured prey, and flying increased over the 5-wk period that young were observed. Kestrels used perch hunting more than other types of hunting and fed exclusively on invertebrates, primarily grasshoppers. Perch hunting success (captures/pounces) increased significantly 3 wk after fledging. After this period there was no significant change. Significant increases in capture rate (captures/hour) occurred 4 and 5 wk after fledging due to increased pounce rates. We observed social hunting among siblings, families, and also among unrelated kestrels. Social hunting occurred during both perch hunting and ground hunting. Social foraging in these kestrels was imitative rather than cooperative.

Desarrollo de los hábitos de cacería en los Halcones Cernícalos

EXTRACTO.—Hemos observado el desarrollo de los hábitos de búsqueda de alimento en Halcones Cernícalos (*Falco sparverius*) con 12 grupos de hermanos. Después de un período de 5 semanas de observación, notamos que estos jóvenes halcones disminuyeron la frecuencia del posarse para descansar, mientras que aumentaron la frecuencia en el posarse para cazar, el comer su presa capturada, y el volar. La cacería desde una percha ocurrió más que otros tipos de cacería. Se alimentaron exclusivamente de invertebrados, principalmente de saltamontes o longostas. El éxito de la cacería desde una posición perchada (captura/embestida) creció significativamente después de 3 semanas de haber dejado el nido. Después de esto no hubo cambio significativo. Un notable incremento en la proporción de capturas (captura/hora) ocurrió entre 4 y 5 semanas después de dejar el nido, y se debió al incremento en la proporción de embestidas. Se observó cacerías en grupos entre hermanos, familias, y también entre individuos sin parentesco. Las cacerías en grupo se realizaron o bien desde el suelo o desde una percha. La provisión de comida en grupo en estos cernícalos fue más bien imitativa que cooperativa.

[Traducción de Eudoxio Paredes-Ruiz]

The post-fledging period, here defined as the period of parental dependency for food in young birds after leaving the nest (see van Tyne and Berger 1966), has received relatively little attention in avian research. This is partly because of the difficulties in observing the behavior of young once they leave the nest (e.g., Brown and Amadon 1968, Newton 1979, Alonso et al. 1987).

The post-fledging period and the subsequent period of recent independence from parents are important life history stages, when young develop foraging skills essential to survival (Weathers and Sullivan 1989). High mortality rates of recently independent juveniles and others during their first year of life reflects the critical nature of this time (e.g., Lack 1954, Henny 1972, Sullivan 1989).

In 1988 we began a study of American Kestrels nesting in nest boxes attached to the backs of highway signs along Interstate Highway 35 (I-35) in Central Iowa. In this paper we describe the development of foraging behavior in young kestrels during the post-fledging phase and during the period of recent independence from parents.

STUDY AREA AND METHODS

Several years prior to the initiation of this study, kestrel nest boxes were attached to the backs of highway signs along I-35 at approximately 2-km intervals, from northern Polk County to northern Worth County in northcentral Iowa. The study area was a corridor approximately 2 km wide on either side of I-35 from 18 km south to 99 km north of Ames. Land bordering I-35 was farmed intensively with row crops.

We banded 97 fledglings observed in 1988 and 1989

with U.S. Fish and Wildlife Service leg bands, and individually marked them with colored vinyl leg jesses before they fledged. We captured 76 percent (35/46) of the adult kestrels in the nest box or with *bal-chatri* noose traps (Berger and Mueller 1959). We banded and individually marked adults with colored vinyl leg jesses.

To locate fledged young for behavioral studies we used the signals from back-mounted radio transmitters (Holohil Systems, Ltd., Woodlawn, Ontario, Canada). We attached transmitters to birds several days before fledging. In 1988 we attached radio transmitters to 12 nestlings in 10 nest boxes. Survival of radio-marked kestrels was high (11 of 12 survived the post-fledging period) and siblings generally maintained close contact for 4 to 5 wk after fledging. This confirmed the technique's usefulness and feasibility for monitoring family group activity. We made observations in 1988 to gain insight into American Kestrel post-fledging behavior and to develop an efficient data recording system. These data are not part of the present analysis.

We tested the transmitters used in 1989 along the highway right-of-way at a height of 1 m. Signal range averaged 2.3 km (N = 13, SD = 0.60, range = 1.1–3.5 km). In 1989, we radio-tagged one randomly selected nestling from each of 13 nests. Young observed in 1989 (50 individuals from 13 nests) fledged between 27 and 31 d after hatching (mean = 29.2, SD = 1.4), from 13 June to 3 July.

One radio-tagged nestling died 7 d after fledging before we could collect behavioral data. We lost signals from 3 of the remaining 12 transmitters within 5 d after the tagged birds fledged. For two of these sibling groups, we were unable to determine whether the transmitters failed or if the individuals left the area. For the third, transmitter failure became evident when we observed the radio-marked kestrel with another sibling group in the study 37 d after fledging. Despite the early loss of signals from these three transmitters, we were able to collect data on behavior of individuals in these broods.

We observed fledglings between 0600 and 1300 H at a distance of 70–100 m with a 20× or 20–60× spotting scope. We did not use a blind because birds under observation frequently changed locations. We monitored fledgling groups on a rotational basis at 1–3 d intervals until we lost contact with the brood. When we could not find a brood, we searched by vehicle an area of approximately 6 km² around their last known location.

We adopted Wyllie's (1985) definition of dispersal, which is movement of a fledged bird farther than 1 km from its nest without return. We determined time of dispersal only for kestrels with transmitters known to be functioning 1 wk after fledging (N = 9).

At the beginning of each observation session, we randomly selected one fledgling, which was not necessarily the one with the transmitter, as the focal bird (Altmann 1974). Two people observed behavior; typically one individual collected data on a sibling group while the other observed another group elsewhere on the study area. In 39 cases two people collected data simultaneously on two birds in the same sibling group, or one person made consecutive observations on different birds in the same sibling group. For analysis, we combined these simultaneous or consecutive observations into one observation session.

Sessions lasted 5 to 60 min or until the focal bird dis-

appeared from view. We did not use data if the bird left in <5 min. We analyzed data for 93 observation sessions (mean length = 57.5 min, SD = 32.0).

A metronome timing device (Wiens et al. 1970), set at 20 sec intervals, cued spot observations of behavior and social activity. At each sound of the tone, we recorded behavior and social activities of the focal kestrel. We recorded four main classes of activity: general behavior, social behavior, hunting behavior, and allopreening and beaking. We recognized nine subclasses of general behavior and five of social behavior.

General Behavior. "Perch resting" describes a kestrel perched and not engaged in any other observed behavior. Rudolf (1982) and Toland (1987) distinguished "perch hunting" from other perching activity by alert posture, erect body or body leaning slightly forward, frequent staring at ground (Fig. 1), and head bobs. Because young kestrels that have never hunted may exhibit some of these behaviors without attempting prey captures, behavior was not recorded as perch hunting until at least one pounce was observed. Flights to/and from the ground and flights between perches during perch hunting bouts were included in perch hunting behavior. We defined "ground hunting" as a bird on the ground searching for prey for >20 sec. Searches of shorter duration involving flight from a perch were considered perch hunting. "Flight" was any non-hunting flight. We use the term "eating" only for kestrels eating self-captured prey. "Maintenance activity" included preening, plumage rousals (shaking), and stretching. "Lying on belly" describes a posture young kestrels often assumed on fenceposts, utility poles, and large tree branches. "Begging" was solicitation of food from parents. "Out of sight" refers to a focal kestrel concealed by vegetation or other objects. A session was discontinued when a bird was out of sight >5 min. "Other" was used to categorize behaviors observed relatively infrequently, and included walking, hover hunting, aggressive interactions among siblings, parent-to-young prey transfers, and eating prey caught by parents. During observation sessions, one or both adults frequently vocalized aggressively at us. We therefore suspect that the interactions with parents occurred less frequently than they would have in the absence of observers.

Social Behavior. Lett and Bird (1987) defined social behavior for American Kestrel fledglings as any behavior which occurred within 2 m of one or more siblings. We adopted this operational definition with two modifications. We extended the distance to 3 m and included non-sibling kestrels in social interactions (adults late in the post-fledging period which no longer feed their young and kestrels from outside the parent/sibling family unit). "Association" was any activity of the focal kestrel except social hunting, which occurred ≤3 m from one or more kestrels. "Social hunting" was hunting activity by the focal kestrel which occurred ≤3 m from one or more kestrels that also were hunting (Fig. 1). "Nonsocial" refers to activity of the focal kestrel occurring >3 m from one or more kestrels. When we could not see whether other kestrels were ≤3 m from the focal kestrel because of dense vegetation we recorded its social status as "Undetermined."

Foraging Behavior. We recorded pounces, captures, and prey type. Foraging success was the percentage of
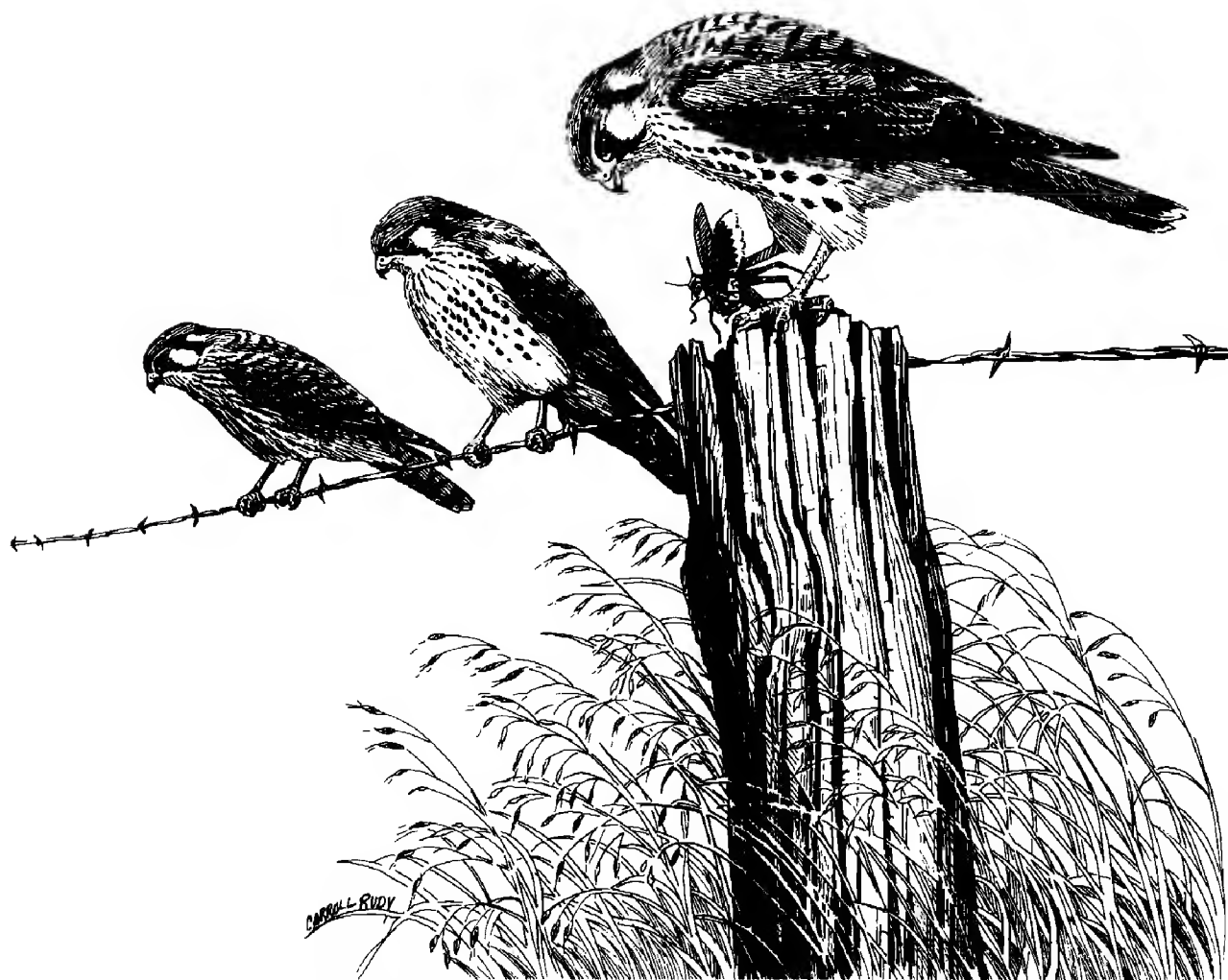
Figure 1. American Kestrels hunting socially after fledging.

pounces with known outcomes that were successful. Out-comes were unknown in 5% of the observed pounces (18/345). We converted pounces and captures to hourly rates based on session length.

Allopreening and Beaking. We recorded the frequen-cies and the individuals involved in allopreening and beak-ing, forms of direct social contact. Allopreening is the preening of a conspecific individual's plumage. Our ob-servations of beaking paralleled those of Sherrod (1983: 182), who adopted the term beaking to describe behavior in young Peregrine Falcons (*Falco peregrinus*) in which "one falcon nibbles at the beak and lore area of its sibling."

Statistical Analysis. We grouped behavioral data ac-cording to 7-d intervals starting with fledging. The ex-perimental unit (n) was the sibling group, and observations of the number of groups observed ranged from 12 during the first wk after fledging to 4 during the fifth. We com-puted statistics for behavior, social, and hunting activity for each sibling group in each 7-d, post-fledging interval for which data were available.

We used the general linear model procedure (PROC GLM, SAS 1985) to obtain an analysis of variance (ANO-VA) and tested for linear trends in specific behaviors dur-ing 5 wk post-fledging. Because not all sibling groups were represented in all weeks and data were missing from some cells, we used Type III sum of squares to calculate P values. We selected 0.05 as the level of significance for linear trends in behavior. Because behaviors were not in-dependent, we adjusted the significance level of P values using Bonferroni's inequalities (Snedecor and Cochran

1989:116). Thus, the level of significance for these tests is 0.05 divided by the total number tests being made on a set of non-independent behaviors.

To compare differences in means for foraging activity between weeks after fledging, we used least significant difference (LSD) t-tests (SAS 1985). We selected 0.05 as the level of significance for t-tests.

RESULTS

Kestrels spent progressively less time inactive and more time foraging as they grew older (Table 1). A significant decrease occurred in perch resting be-havior ($P < 0.001$) with weeks post-fledging, where-as significant increases occurred in perch hunting ($P < 0.001$), eating self-captured prey ($P < 0.001$), and flying ($P < 0.002$). We did not observe young eating prey captured by their parents after the third week post-fledging. Mean time of dispersal for ra-dio-marked kestrels ($N = 9$) was 23.6 d after fledg-ing.

Perch hunting constituted a greater percentage of foraging time than ground hunting in all 5 wk post-fledging (Table 1). Significant increases occurred with time in perch hunting pounces ($P < 0.001$), captures ($P < 0.001$), and success ($P < 0.05$; Fig.

Table 1. Time (mean % ± SE) spent engaged in 10 behavior categories by post-fledging American Kestrels in Iowa.

	WEEKS POST-FLEDGING					
BEHAVIOR	1 MEAN ± SE	2 MEAN ± SE	3 MEAN ± SE	4 MEAN ± SE	5 MEAN ± SE	1–5 P-VALUES[a]
Perch resting	75.3 ± 4.0	53.8 ± 5.2	41.4 ± 3.3	19.5 ± 7.2	23.8 ± 2.1	<0.0010
Perch hunting	0.2 ± 0.2	6.0 ± 2.0	18.3 ± 2.7	43.4 ± 8.8	48.6 ± 2.8	<0.0010
Ground hunting	0.0	0.9 ± 0.7	3.6 ± 1.6	10.0 ± 5.4	1.8 ± 1.1	0.0580
Flying	0.4 ± 0.1	2.1 ± 0.4	3.9 ± 0.9	5.8 ± 3.3	7.5 ± 2.6	0.0018
Eating self-captured prey	0.0	<0.1 ± 0.1	1.5 ± 0.8	6.6 ± 2.6	7.9 ± 0.8	<0.0010
Maintenance	14.5 ± 2.0	19.1 ± 4.2	17.4 ± 3.4	9.3 ± 3.8	8.7 ± 0.8	0.3215
Lying on belly	4.1 ± 3.2	7.3 ± 4.1	2.9 ± 1.6	0.0	0.0	0.1750
Begging	1.7 ± 1.1	2.5 ± 0.6	2.6 ± 0.9	0.0	0.0	0.1394
Out of sight	2.3 ± 0.9	5.4 ± 1.2	7.9 ± 2.4	5.3 ± 1.6	1.6 ± 0.6	0.1794
Other	1.4 ± 0.4	2.8 ± 1.4	0.4 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.0547

[a] P-values are based on ANOVA F-tests for linear trends across 5 wk post-fledging (df = 1, 27). All tests for lack of fit were not significant ($P > 0.05$).

2). Ground hunting success also increased significantly ($P < 0.01$).

We identified nearly all prey items caught by young kestrels as grasshoppers (order Orthoptera). We saw one kestrel feeding on a dragonfly (order Odonata), and some items were too small to identify.

During four sessions we observed seven brief bouts of hover hunting in birds 12–37 d post-fledging. None of these attempts were successful. We observed five flycatching attempts (see Suring and Alt 1981) among birds 23–25 d post-fledging during three sessions, four were successful.

When perch resting, fledged kestrels became progressively less social with time. The significant decrease in association ($P < 0.001$) and the significant increase in nonsocial behavior ($P < 0.001$; Table 2) reflect this trend.

Allopreening and beaking exchanges occurred

Table 2. Time (mean % ± SE) spent engaged in social and nonsocial activity by post-fledging American Kestrels in Iowa.

BEHAVIOR BY SOCIAL ACTIVITY	WEEKS POST-FLEDGING					1–5 P-VALUES[a]
	1	2	3	4	5	
Perch resting (N)[b]	(12)	(10)	(10)	(6)	(4)	
Association	57.7 ± 10.8	48.9 ± 8.2	38.3 ± 6.0	25.8 ± 16.3	13.5 ± 8.2	<0.0010
Social hunting	—	—	—	—	—	—
Nonsocial	28.2 ± 7.5	48.9 ± 8.1	56.1 ± 5.8	74.2 ± 16.3	86.5 ± 8.2	<0.0010
Undetermined	14.1 ± 8.6	2.2 ± 1.0	5.6 ± 3.3	0.0	0.0	0.2722
Perch hunting (N)	(1)	(6)	(10)	(6)	(4)	
Association	0.0	17.3 ± 11.7	19.4 ± 6.8	6.6 ± 6.0	3.3 ± 1.7	0.1658
Social hunting	0.0	11.6 ± 5.3	21.3 ± 7.1	30.4 ± 16.2	14.5 ± 8.4	0.0772
Nonsocial	100.0	69.8 ± 12.5	53.0 ± 6.1	63.0 ± 18.3	82.2 ± 8.5	0.4673
Undetermined	0.0	1.3 ± 0.8	6.3 ± 4.9	0.0	0.0	0.7646
Ground hunting (N)	(0)	(5)	(7)	(5)	(3)	
Association	0.0	15.0 ± 15.0	21.7 ± 10.3	1.2 ± 1.2	0.0	0.0955
Social hunting	0.0	20.4 ± 13.6	33.6 ± 13.9	45.9 ± 22.7	0.0	0.9385
Nonsocial	0.0	44.6 ± 17.5	44.6 ± 8.4	52.9 ± 22.1	100.0	0.4887
Undetermined	0.0	20.0 ± 20.0	0.0	0.0	0.0	—

[a] P-values are based on ANOVA F-tests for linear trends across 5 wk post-fledging. Perch resting df = 1, 26; perch hunting df = 1, 12; hunting on ground df = 1, 7. All tests for lack of fit were not significant ($P > 0.05$).
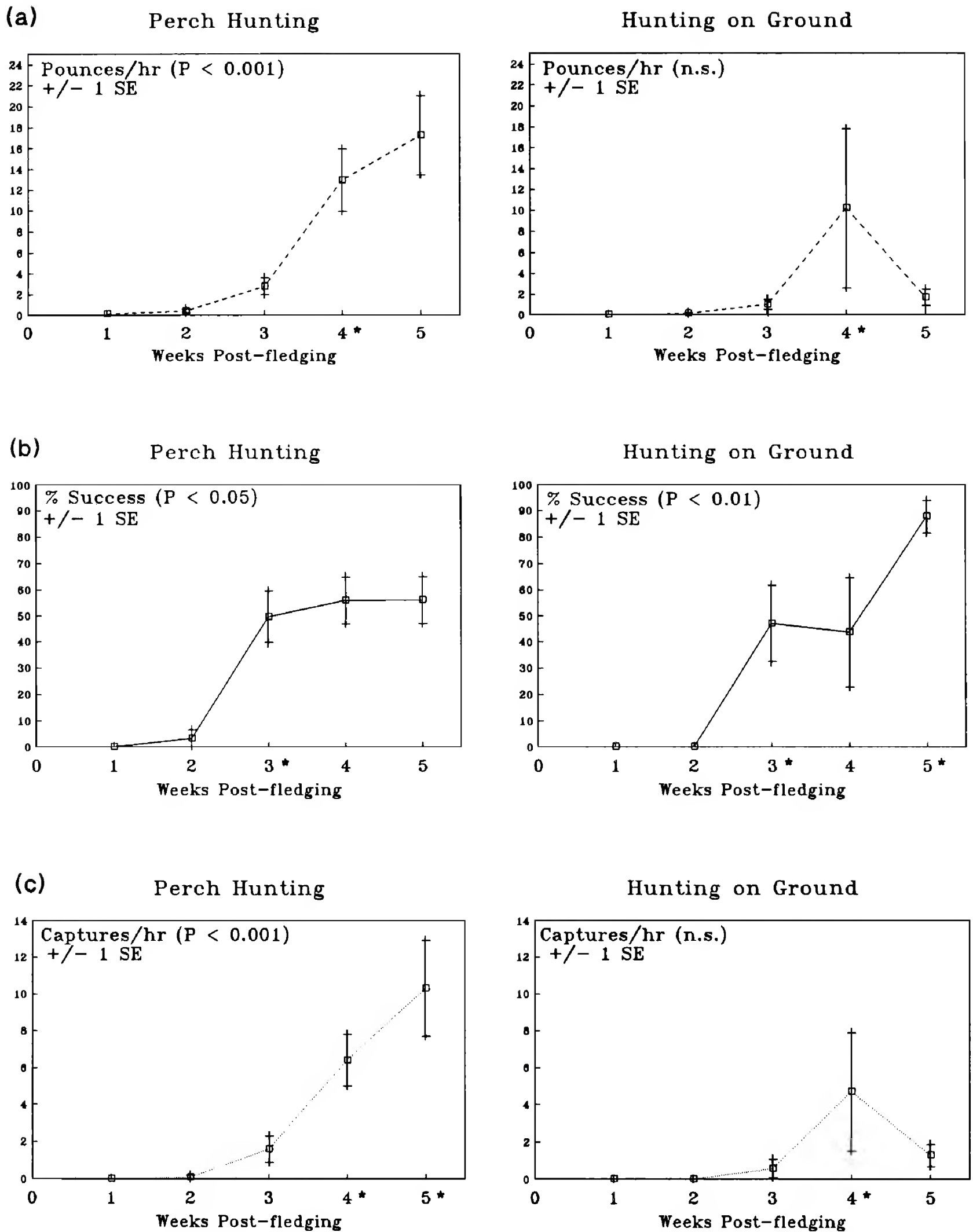[b] Number of sibling groups observed.

Figure 2.   Mean foraging pounce (a), percent success (b), and capture rates (c) for post-fledging American Kestrels at weekly intervals. P values are based on ANOVA F-tests across 5 wk post-fledging (perch and ground hunting pounce and capture rate df = 1, 27; perch and ground hunting success df = 1, 10). Weekly means with * differ significantly ($P < 0.05$, least significant difference t-test) from the preceding week.

during 15% (14/93) of the sessions. We observed the behaviors in 9 of 12 family groups among young ranging from 3–23 d post-fledging.

Kestrels were social while perch and ground hunting and spent a substantial amount of time in these activities (Table 2). We observed social hunting during 41% (20/49) of the sessions in which hunting occurred. We saw social hunting in 10 of 12 sibling groups and quantified it in 8. In three of these eight groups, social hunting involved siblings and nonsiblings. We saw extra-familial social hunting in 20% (4/20) of the sessions with social hunting. In one of these groups we observed social hunting involving siblings, a parent, and a non-sibling female of unknown age. The female parent did not feed the young but called and flew aggressively at a Red-tailed Hawk (*Buteo jamaicensis*) perched within 20 m of the group, causing the hawk to leave the area. Social hunting among non-sibling groups occurred just before or after dispersal from the natal area. We observed social hunting on one or two occasions and then lost contact due to signal loss from the radio-tagged kestrel. We are uncertain whether these groups remained together.

DISCUSSION

Association. Association among fledgling kestrels occurred mostly during the first 2 wk after fledging, when young are most dependent on parents. Moreno (1984) found that fledgling Northern Wheatears (*Oenanthe oenanthe*) fed by one parent perched closer to each other than fledglings fed by both parents, and that a tendency for fledglings to associate (perch <1 m apart) diminished as they became increasingly more independent. Distance between sibling Spanish Imperial Eagles (*Aquila heliaca*; Alonso et al. 1987) and Black Kites (*Milvus migrans*; Bustamante and Hiraldo 1990) increased with age, and there was a positive correlation between increased sibling distance and flying proficiency.

Wittenberger (1981) suggested that the allopreening in breeding birds is important in maintaining pair bonds. Our observations of allopreening and beaking provide evidence that American Kestrels are social after fledging. Thus, fledgling kestrels do not perch close together merely to improve their chances of being fed or because they lack flying skills. We suggest allopreening and beaking may maintain social bonds between siblings during the post-fledging period. Both behaviors occur in the social repertoire of fledgling Peregrine Falcons (Sherrod 1983), and

Komen and Meyer (1989) observed allopreening in fledgling Common Kestrels (*Falco tinnunculus*). Other researchers have reported close associations among fledged American Kestrels (Sherman 1913, Cade 1955, Roest 1957, Smith et al. 1972, Balgooyen 1976, Wheeler 1979, Lett and Bird 1987), but we have not found any reference in the literature to allopreening or beaking.

Development of Foraging Behavior. Bird and Palmer (1988) described various foraging methods used by American Kestrels. Toland (1987) grouped American Kestrel foraging methods into three categories: perch hunting (which he observed 70–97% of the time); hover hunting (2–20%); and horizontal flight (<5%). The American Kestrel is a generalist predator of invertebrates and small vertebrates, and its diet varies with season and geographic area (Heintzelman 1964, Bent 1938).

In this study, young kestrels progressed from relative inactivity to active foraging within 3 to 4 weeks of leaving the nest (Fig. 2, Table 1). The two hunting methods observed most frequently, perch hunting and ground hunting, were probably least dependent on flying ability. Early reliance on hunting techniques requiring relatively simple flight patterns has been reported for post-fledging Common Kestrels (Shrubb 1982), Peregrine Falcons (Sherrod 1983), Red-tailed Hawks (Johnson 1986), Northern Wheatears (Moreno 1984), and Spotted Flycatchers (*Muscicapa striata*; Davies 1976).

Fledged American Kestrels fed on easily-caught invertebrate prey. Dunstan (1970), Johnson (1986) and Shrubb (1982) reported invertebrates as the earliest prey of Great Horned Owls (*Bubo virginianus*), Red-tailed Hawks, and kestrels. Toland (1987) found an 82% success rate among American Kestrels (both sexes, all ages) hunting invertebrates, with lower rates for rodents (66%) and birds (33%). Collopy (1973) reported that kestrels wintering in California had 64% hunting success for invertebrates and 25% for vertebrates. Smallwood (1987) found kestrels wintering in Florida fed only on arthropods, with comparable success rates for males (76%) and females (73%).

In this study, mean perch hunting success increased significantly from 3.3% in the second week after fledging to 49.7% in the third, but did not change significantly thereafter (Fig. 2). These success rates for invertebrates are substantially lower than rates cited above and indicate that kestrels further develop their foraging skills after dispersal. We

observed significant increases in mean capture rates by perch hunting kestrels at 4 and 5 wk post-fledging due to increased pounce rates (Fig. 2). The observed increases in perch hunting success and pounce rates may be at least partially due to increases in grasshopper density during the post-fledging period. Grasshoppers were abundant in central Iowa in July and August 1989 (Rice 1989).

Reports of increasing numbers of kills by maturing Peregrine Falcons released from hack sites (Sherrod 1983) and increasing hunting success with age in fledged Red-tailed Hawks (Johnson 1986) were supported by few quantitative data. Increased hunting success over time was quantified for fledgling Ospreys (*Pandion haliaetus*; Edwards 1989a) and passerines, including Northern Wheatears (Moreno 1984), Spotted Flycatchers (Davies 1976), and Yellow-eyed Juncos (*Junco phaeonotus*; Sullivan 1988).

Social Hunting. Wilson (1975:51) described two types of social foraging, imitative and cooperative. The net effect of such social hunting probably is greater foraging efficiency.

During imitative foraging, individuals observe others in the group and may initiate, copy, increase, or learn foraging behavior. All of these may occur during social hunting but are difficult to differentiate. Communication among imitative foragers probably is indirect, and group members do not coordinate their efforts during the hunt. Several investigators reported feeding benefits associated with imitative foraging (e.g., Krebs 1973, Rubenstein et al. 1977, Sullivan 1984). Edwards (1989a, 1989b) compared the foraging behavior of sibling pairs of Ospreys and single young and found that pairs and singles both reached the same level of success but that siblings developed their skills sooner. Sibling pairs also used similar foraging techniques and had similar diets. Edwards suggested these differences were a result of observational learning between siblings.

Hector (1986) listed six characteristics distinguishing cooperative foraging from imitative foraging, including division of labor and use of signals to coordinate movements. He reported that mated pairs of Aplomado Falcons (*Falco femoralis*) cooperatively hunting for birds had greater success (45%) than when alone (21%). Group size in cooperatively foraging Harris' Hawks (*Parabuteo unicinctus*) was positively correlated with capture (Bednarz 1988).

After the breeding season American Kestrels may hunt in social groups of 10–20 juveniles and adults

(Cade 1955, Wheeler 1979, Wilmers 1982). We also observed post-breeding adults and juveniles hunting in groups, but social hunting was observed most frequently among siblings prior to or just after dispersal. Young kestrels hunted socially from 12–46% of the time (Table 2). We saw nothing to indicate that individuals in groups were coordinating their efforts or using signals to coordinate movements. Thus, social foraging in these kestrels was imitative rather than cooperative.

We considered the possibility that differences might exist between the hunting efficiency of kestrels hunting socially and those hunting nonsocially, but the study design was not adequate to test this idea. Further research is needed to document whether social hunting influences foraging efficiency in the American Kestrel.

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SHORT COMMUNICATIONS

NEST SITE AND PREY OF A PAIR OF SHARP-SHINNED HAWKS IN ALBERTA

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Sharp-shinned Hawks (*Accipiter striatus*) nest mainly in coniferous and mixed coniferous/deciduous forests (Platt 1976, Evans 1982, Reynolds et al. 1982) where they prey on small to medium-sized birds (e.g., Snyder and Wiley 1976, Duncan 1979, Reynolds and Meslow 1984). Information on prey delivered to the nest is available from few regions within this hawk's range. Here I present data on the food habits of a pair of Sharp-shinned Hawks in the aspen parkland of Alberta, and describe their nesting habitat.

METHODS

I found the Sharp-shinned Hawk nest containing three young on 6 July 1987, 0.6 km from the southeast shore of Beaverhill Lake, Alberta (53°24'N 112°31'W). Based on size and feather development (Brown and Amadon 1968), I judged the young to have hatched about 27 June. The nest was observed from a blind 6.6 m east of the nest tree during 18 observation periods, from 14–24 July. Observation periods were 1.5–2.0 hr long for a total of 31 hr of observation. The adult male and female could be distinguished by size, plumage, and after 2 d of observation, by vocalization. I identified prey items, as well as which adult caught and delivered the prey, for each observed feeding. I compared prey remains (mainly feathers) found in or below the nest to specimens in the University of Alberta Zoology Museum collection.

RESULTS

The Sharp-shinned Hawks had three young and one egg that did not hatch. After fledging on 20 July and 22 July, the hawks continued to use the nest as a feeding site for at least 5 days. Young were seen in the immediate vicinity of the nest until 7 August.

The Sharp-shinned Hawks nested in deciduous forest. The nest was 2.4 m high in a stunted Trembling Aspen (*Populus tremuloides*; height = 4.5 m). The nest was concealed within a dense stand of willows (*Salix* spp.; 65,820 stems/ha, $\bar{X}$ height = 3.5 m). Canopy closure was 82.5%. Horizontal cover at heights up to 3 m (Noon 1981) ranged from 74–100%. Forest tent caterpillars (*Malacosoma distria*) reduced foliage density throughout the nesting period. The ground below the nest was ephemerally wet.

Sixteen of the deliveries to the nest were by the female,

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3 by the male, and 2 were undetermined. The adult female rarely left the nest area whereas the male was rarely seen there. Prey transfers were initiated by the male calling from about 20 m south of the nest. The female then flew toward the male and returned within 1 min with prey.

I observed the male Sharp-shinned Hawk hunting on four occasions. Two were unsuccessful attempts to capture fledgling Red-winged Blackbirds (*Agelaius phoeniceus*). The other two observations were at dusk when the hawk caught two large moths in flight.

Twenty-one prey items were delivered to the nest in 31 hr of observation: 20 birds and one small mammal resembling a vole (*Microtus* sp.). I was able to identify 12 of the 21 items to species. Six were fledgling Red-winged Blackbirds and one each of Yellow Warbler (*Dendroica petechia*), American Goldfinch (*Carduelis tristis*), flycatcher (*Empidonax* sp.), American Robin (*Turdus migratorius*) and a Tree Swallow (*Tachycineta bicolor*). In addition, prey remains consisted of Black-billed Cuckoo (*Coccyzus erythropthalmus*), flycatchers (*Empidonax* sp.), Purple Martin (*Progne subis*), Black-capped Chickadee (*Parus atricapillus*), House Wren (*Troglodytes aedon*), Veery (*Catharus fuscescens*), American Robin, Savannah Sparrow (*Passerculus sandwichensis*), Clay-colored Sparrow (*Spizella pallida*), Red-winged Blackbird, American Goldfinch, Yellow Warbler, Tree Swallow, Downy Woodpecker (*Picoides pubescens*), Wilson's Phalarope (*Phalaropus tricolor*), and Meadow Vole (*Microtus pennsylvanicus*).

I found 14 celluloid color bands in regurgitated pellets. These bands were from fledgling House Wrens studied in the same area (Quinn 1989). No bands from adult House Wrens were found, although the majority of the population had been banded (74% of known breeding population). The Sharp-shinned Hawk nest was located on the west edge of a 7.65 ha study grid containing 71 nest boxes, 50 of which were occupied by House Wrens.

DISCUSSION

The tree species composition and height of canopy at the Beaverhill Lake nest-site differed from those previously described in the literature (Platt 1976, Reynolds et al. 1982). There were no conifers within 5 km of the nest and the crown height of the nest tree was only 4.5 m. Similarities in nesting habitat between the Beaverhill Lake nest and those previously reported are the high vegetation density, well developed canopy, mesic conditions and close proximity to water.

The dominance of avian prey in the present study is consistent with previously reported data (Snyder and Wi-

ley 1976, Duncan 1979). The relatively high number of juvenile Red-winged Blackbirds and especially House Wrens in the prey sample suggests selection for juvenile birds.

RESUMEN.—Una pareja de Gavilán Pechirrojo Menor (*Accipiter striatus*), en época de anidar, ha sido observada cerca de Beaverhill Lake, Alberta. El nido estaba ubicado a 2.4 m sobre el suelo en un bajo Alamo Temblón (*Populus tremuloides*) dentro de una área densa de sauces (*Salix* spp.). La hembra puso cuatro huevos, tres de los cuales incubaron bien, y las crías emplumaron hasta volar. El macho fue el que hizo la mayoría de la caza, haciendo presa, predominantemente, de jóvenes Tordos Sargento (*Agelaius phoeniceus*) y de Trogloditas Continental (*Troglodytes aedon*). Se observó que el macho capturaba y consumía grandes polillas.

[Traducción de Eudoxio Paredes-Ruiz]

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ORNATE HAWK-EAGLE FEEDING ON GREEN IGUANA

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The Ornate Hawk-eagle (*Spizaetus ornatus*) is a scarce resident of dense subtropical and tropical forests from southern Mexico to northern Argentina (Eitniear 1986, 1988, Brown and Amadon 1968). The species is stated to be the rarest of the three hawk-eagles in Belize (Hartshorn el al. 1984). Lyon and Kuhnigk (1985) documented both mammalian and avian prey species but considered the Ornate Hawk-eagle a specialist on birds. This note doc-

uments an additional sighting of the species feeding on Green Iguanas (*Iguana iguana*) in Belize.

On 28 May 1990, we observed an Ornate Hawk-eagle feeding on a Green Iguana while perched in a tree on the banks of the Raspaculo branch of the Rio Guacamayo, 4 km upstream from the confluence of the Raspaculo and Guacamayo. Several minutes after our arrival the hawk-eagle attempted to carry the prey to another branch in a nearby tree. The hawk-eagle was unable to lift the iguana, however, and both plummeted into the underbrush, where the hawk-eagle continued to feed on the lizard. The entire episode was documented on video tape, which is deposited in the video library of the Center for the Study of Tropical Birds, Inc. An earlier sighting was made by Mick Fleming in the fall of 1987. In the same area as the 1990 sighting, Fleming's party observed an Ornate Hawk-eagle flying across the Raspaculo with an adult Green Iguana in its talons. The bird alighted in a nearby tree where it consumed its prey (Fleming 1987).

In Tikal National Park, 70–80 km northwest of the Raspaculo River, Lyon and Kuhnigk (1985) observed Ornate Hawk-eagles feeding upon a young tinamou (Tinamidae), a Plain Chachalaca (*Ortalis vetula*), a young Crested Guan (*Penelope purpurascens*), a Gray-headed Dove (*Leptotila plumbeiceps*) and a leaf-nosed bat (Phyllostomidae). More recently, also in Tikal National Park, Flatten et al. (1989) recorded 52 Ornate Hawk-eagle prey items of which 21 (40.4%) were identified as avian, 24 (46.1%) as mammalian, and 7 (13.5%) were unidentifiable. Klein et al. (1988) reported that 63.5% of prey items were avian, including macaws (*Ara* spp.). The Ornate Hawk-eagle has been reported to feed upon Great Curassow (*Crax rubra*) (Russell 1964), Kinkajoo (*Potus flavus*) (Brown and Amadon 1968), and Guiana Cock-of-the-Rock (*Rupicola rupicola*) (Trail 1987). An additional report of this species feeding on a reptile was made by Klein et al. (1988) who mentioned that the hawk-eagle fed upon an unidentified snake and a lizard (Teiidae) in Manaus, Brazil.

Since previous studies of this raptor have not been conducted along rivers where Green Iguanas are abundant, our sighting (despite abundant avian prey items) suggests that the Ornate Hawk-eagle, like most raptors, will take vulnerable prey species when they become available. Therefore, the Ornate Hawk-eagle should be considered more opportunistic than previously believed.

RESUMEN.—Los autores observaron un Aguila Elegante (*Spizaetus ornatus*) consumir una iguana (*Iguana iguana*) en Belice. Se considera que esta especie se alimenta principalmente de aves. Sin embargo, este registro, así como los dos documentados y publicados previamente, indican que el águila exhibe el mismo comportamiento oportunista documentado en aves rapaces que habitan zonas de clima templado del norte.

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NOTES ON A SUCCESSFUL NESTING BY A PAIR OF YEARLING PEREGRINE FALCONS (*Falco peregrinus*)

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It is rare for yearling male Peregrine Falcons (*Falco peregrinus*) to breed; occasionally an immature female will pair with an adult male. When yearlings attempt to breed, many fail to produce eggs or lay a smaller than normal clutch; if eggs are produced, young seldom fledge (Hagar 1965, Hickey 1965, Cade 1982, Mearns and Newton 1984, Ambrose and Riddle 1988, Newton and Mearns 1988). In Milwaukee, Wisconsin, in 1988, a pair of yearling peregrines produced and fledged young. This is the first known record of successful nesting by a pair of yearlings.

STUDY SITE

The First Wisconsin Center, overlooking Lake Michigan, is the tallest building in Wisconsin. The top floor is an observation deck, with full length glass windows on all sides. The nest was in a hack box (Sherrod et al. 1982) that had been installed on a 2 m ledge outside the windows on the west side of this floor, 178 m above street level. Fourteen young peregrines had been released from the site in 1987.

HISTORY OF FALCONS

The male of the pair, a *F. p. pealei* × *F. peregrinus*, had been released in 1987 in Ft. Sheridan, Illinois, with 10 other youngsters. He was described as a dominant bird (J. McCoy and M. Spreyer, *in litt.*). The female, a *F. p. anatum*, was one of 20 young released in Rochester, Minnesota, in 1987.

BREEDING ACTIVITY

A peregrine was seen hunting near the First Wisconsin Center on 21 March 1988. Within 10 d a second falcon had joined it. Both birds were in juvenile plumage, except for a spattering of adult feathers on their backs and a fair amount of white on the crop area. Both falcons molted quickly. By mid-June they looked adult, especially from a distance. By July, their heads, backs and well over 75% of their undersides had molted and they were replacing their flight feathers.

Both falcons were seen regularly through 18 May. We inspected the hack box on 13 May, but found no evidence of nesting. When sightings stopped abruptly after 18 May, we thought the pair had left the area. But on 15 June we found the female in the hack box brooding two new chicks, one male and one female. These were the first peregrines hatched in the wild in Wisconsin in over 20 years.

Because of precarious footing in front of the hack box, we feared for the safety of the nestlings so we barred the front of the box on 10 July. The parents continued to feed the young through the bars. We added two captive-produced chicks on 15 July. We banded all four chicks, color-marked them with fluorescent spray paint, and released them from the box on 26 July, at an age of 38-42 days.

All four young fledged. The male was strongly aggressive toward the young, stooping and striking once they were in the air or when they perched on exposed ledges. His attack was particularly intense when the flight of the young falcons appeared unsteady; at times he actually knocked them out of the air. Although stooping became less intense with time, each fledgling was driven to the ground at least once. While stooping, the male often gave creaking calls as described by Ratcliffe (1980).

One youngster broke a femur when it hit the ground after an attack and later died of complications. Another died after hitting a glass window. The third youngster was injured twice, but survived and was relocated to a hack site in Omaha, Nebraska. The fourth stayed in Milwaukee and was last seen in early September.

DISCUSSION

Most reports of juvenile peregrines attempting to breed come from relatively recent observations of an expanding, reintroduced population. As Hunt (1988:673) pointed out, "There is little information on the ecological age of first breeding in stable, undisturbed populations of peregrines." Competition for nest sites has been recognized as a factor limiting the number of breeding yearlings. From 1935-1957, Hagar (1969) observed only one mated juvenile female on a highly rated cliff; six others were found on low rated cliffs. None of these seven nests were successful. Today, tall buildings in cities are providing more high-quality nest sites, and without a stable population of adult peregrines, these sites are available for juveniles to attempt to nest.

Newton and Mearns (1988) suggest that breeding might be delayed because juveniles that are inefficient foragers or are confined to areas where prey is scarce cannot develop the body reserves necessary to breed and cannot afford to spend time defending a territory. This is especially true for young males, for whom the increased burden of feeding a mate and family requires well developed hunting skills. The western shore of Lake Michigan is a well-documented migration route, and the availability of prey may have

played a role in the pair of falcons selecting Milwaukee as a nest site and breeding successfully as yearlings.

According to Ratcliffe (1980:341), paired juveniles "are often in transitional plumage, with a mixture of dark brown and slate grey." He also noted that breeding adults "do not usually begin to molt until nesting is well advanced or actually over." Our juvenile pair molted very quickly; both looked adult by the time the eggs had hatched, especially when viewed from a distance. We agree with Ambrose and Riddle (1988:680), who feel that "there may be other cases of one year old birds attempting to breed which were not detected because of their nearly adult plumage." It is possible that the hormone levels necessary to initiate and maintain breeding behavior might affect the rate at which mated juveniles attain their adult plumage.

Skutch (1976) suggests that when parent birds drive fledglings from the air or from exposed perches, this may be a response that reduces detection by predators. Also, "surviving subadult falcons which returned to hack sites from the preceding year appeared to react somewhat like parents with this respect. The aggressive stoops by which the subadults forced the young down, however, were of a more serious nature, and they often hit the youngsters a forceful blow. The stimulus in this case seems to be a 'new falcon' flying in the area, and aggression is the response" (Sherrod 1983:144).

The young age of the male in our study may well have caused his strongly aggressive behavior. We do not know if adding the bars to the hack box contributed to his aggression by limiting his contact with the chicks, but had the young left the box prematurely, they might have been knocked off the ledge by the male's attacks before they were old enough to fly. As a breeding adult, the male also harassed his fledged young when their flight appeared weak, but never with the same intensity and we never again saw him strike them forcefully.

RESUMEN.—En 1988, en Milwaukee, Wisconsin, una pareja de Halcones Peregrinos (*Falco peregrinus*) de aproximadamente un año de edad, incubó y crió hasta que las crías pudieran volar; siendo éste, el primer caso que conocemos de una nidada con logros positivos. La pareja cambió de plumaje rapidamente; a mediados de junio, y especialmente a la distancia, los dos tenían la apariencia adulta. El macho se mostró agresivo con sus crías, lanzándose hacia ellos y golpeándoles fuertemente.

[Traducción de Eudoxio Paredes-Ruiz]

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NON-BREEDING SEASON DIET OF LONG-EARED OWLS IN MASSACHUSETTS

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The Long-eared Owl (*Asio otus*) is a widely-distributed, holarctic species (Burton 1973). In Massachusetts, Long-eared Owls are a species of special concern and little is known of their distribution, biology and ecology (Melvin et al. 1989).

Long-eared Owl food habits have been extensively studied in North America (Marti 1976, Marks 1984), and Europe (Nilsson 1981, Wijnandts 1984, Cramp 1985). At least 23 800 prey items in North America (Marti 1976) and over 360 000 prey items in Europe (Wijnandts 1984) have been identified. To our knowledge, nothing has been published on the diet of these owls in Massachusetts. We located only one study in Connecticut, which reported diet of this species for New England (Choate 1971). Here, we compare non-breeding season diet of Long-eared Owls from two locations in Massachusetts.

Pellets were collected from Nantucket Island and the mainland town of Belmont, approximately 176 km apart. Nantucket Island (130 km²) is composed of moraines and out-wash plains from Pleistocene glaciation (Woodsworth and Wigglesworth 1934). It is also unique in its composition of maritime heaths or "moorlands" (Tiffney and Eveleigh 1985). Belmont is a densely settled suburban town approximately 12 km west of Boston. The topography is geologically a drumlin, dominated by deciduous woods with pockets of conifers. Abandoned orchards and large meadows occur throughout the woodlands.

The owls' non-breeding season was defined as 1 August to 1 April. Owls were observed at roost sites after detection of their pellets or "whitewash." Pellets were collected between November 1984 and February 1985 at irregular intervals. Pellets were air dried for four weeks and then dissected. Prey items were identified by comparing skulls, mandibles, long bones and feathers with museum specimens.

Differences in frequencies of prey between sites were tested using a chi-square test of independence (Siegel 1956). Dietary overlap between sites was calculated using Schoener's (1968) symmetric index. Food niche-breadth was calculated using the antilog of the Shannon-Wiener equation (see Marti 1987). Biomass was calculated using midpoints of weight ranges reported by Godin (1977) for mammals and Dunning (1984) for birds. We used mid-

points because weights of prey can vary with habitat, season, age and sex. Mean weights reported in the literature are most often those of adult specimens and could lead to overestimates of biomass calculations.

Three owls were observed at each roost site. The Nantucket roost was in a dense stand of White Pine (*Pinus strobus*) forest, within 1 km of open moorlands and beach grasslands. The Belmont roost was in a Pitch Pine (*Pinus rigida*) stand, within a mixed deciduous/coniferous forest, and within 0.5 km of meadows and orchards. Smith (1981) and Bosakowski (1984) stated that Long-eared Owls prefer dense stands of coniferous trees. Bosakowski (1984) felt foliage density may afford protection from environmental factors and predation. Our roost sites were also in dense cover.

We recorded 915 prey items from two study sites (Table 1). Four species of mammals and two species of birds were identified. Meadow voles (*Microtus pennsylvanicus*) were the most numerous prey by number and biomass (Table 1). This is consistent with other studies (Marti 1976, Nilsson 1981, Marks 1984, Wijnandts 1984). Choate (1971) reported 91% (N = 128) meadow voles in the Long-eared Owl diet from Connecticut, the only New England study.

Between the two locations, the owls had similar diets (overlap = 99.2%); however, prey species proportions differed significantly (χ^2 = 28.4, df = 3, $P < 0.005$). This was due to higher proportions of white-footed mice (*Peromyscus leucopus*) from Nantucket owls and higher proportion of short-tailed shrews (*Blarina brevicauda*) from Belmont owls (Table 1). Food niche-breadth values were similar from the two sites (1.85 at Nantucket and 1.89 at Belmont) and were in the range of values reported for North American Long-eared Owls that feed primarily on voles (1.60–2.30; see Marks 1984).

RESUMEN.—Las dietas de buhos de la especie *Asio otus*, en la estación no reproductiva, en dos áreas de estudio en Massachusetts, han sido determinadas por medio del análisis de egagrópilas. Novecientos quince items conteniendo residuos de presa han sido identificados. En la Isla Nantucket, la dieta (N = 657) estuvo constituída en el 79% por ratones de la especie *Microtus pennsylvanicus*,

Table 1. Non-breeding season diet of Long-eared Owls in Massachusetts. Prey weights (g) are given in parentheses.

SPECIES	NANTUCKET				BELMONT			
	No.	%	BIOMASS	%	No.	%	BIOMASS	%
Meadow Vole (20–64)	516	78.5	21 672	87.6	206	79.8	8652	88.6
White-footed Mouse (16–29)	122	18.6	2684	10.8	26	10.1	572	5.8
Short-tailed Shrew (12–24)	12	1.8	216	0.9	19	7.4	342	3.5
Meadow Jumping Mouse (13–23)	4	0.6	72	0.3	0			
Blue Jay (64–109)	1	0.2	86	0.3	1	0.4	86	0.9
Northern Flicker (92–129)	0				1	0.4	110	1.1
Unid. Birds	2	0.3	—	—	5	1.9	—	—
Totals	657	100.0	24 730	99.9	258	100.0	9762	99.9

mientras que el 19% correspondió a ratones de la especie *Peromyscus leucopus*. En Belmont, la dieta (N = 258) estuvo constituída en el 80% por ratones de la especie *M. pennsylvanicus*, 10% correspondió a ratones de la especie *P. leucopus*, y 7% a musarañas de la especie *Blarina brevicauda*. Los buhos de cada una de las áreas de estudio mostraron dietas similares en un 99.2%. Sin embargo, hubo diferencia significativa en la proporción de las especies de presa capturada.

[Traducción de Eudoxio Paredes-Ruiz]

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